S-NA-Lawrence

UNIVERSITY OF KANSAS
MUSEUM OF NATURAL HISTORY

MISCELLANEOUS
PUBLICATION
NO. 65

The Biology of an Equatorial Herpetofauna in Amazonian Ecuador

By
William E. Duellman

UNIVERSITY OF KANSAS
LAWRENCE 1978

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

The University of Kansas Publications, Museum of Natural History, beginning with volume 1 in 1946, was discontinued with volume 20 in 1971. Shorter research papers formerly published in the above series are now published as Occasional Papers, Museum of Natural History. The Miscellaneous Publications, Museum of Natural History, began with number 1 in 1946. Longer research papers are published in that series. Monographs of the Museum of Natural History were initiated in 1970. All manuscripts are subjected to critical review by intra- and extramural specialists; final acceptance is at the discretion of the publications committee.

Institutional libraries interested in exchanging publications may obtain the Occasional Papers and Miscellaneous Publications by addressing the Exchange Librarian, University of Kansas Library, Lawrence, Kansas 66045. Individuals may purchase separate numbers of all series. Prices may be obtained upon request addressed to Publications Secretary, Museum of Natural History, University of Kansas, Lawrence, Kansas 66045.

THE UNIVERSITY OF KANSAS
MUSEUM OF NATURAL HISTORY

MISCELLANEOUS PUBLICATION NO. 65
August 30, 1978

The Biology of an Equatorial Herpetofauna in Amazonian Ecuador

BY

WILLIAM E. DUELLMAN

Curator
Division of Herpetology
Museum of Natural History
Professor
Department of Systematics and Ecology
The University of Kansas
Lawrence, Kansas 66045 U.S.A.

Publication Supported by a Grant from the
National Science Foundation
(DEB 77-28380)

THE UNIVERSITY OF KANSAS
LAWRENCE
1978

University of Kansas Publications, Museum of Natural History

Editor: Linda Trueb

Miscellaneous Publication No. 65
pp. 1-352; 198 figures; 34 tables
Published August 30, 1978

Museum of Natural History
The University of Kansas
Lawrence, Kansas 66045
U.S.A.

Printed by
University of Kansas Printing Service
Lawrence, Kansas

CONTENTS

PLATES FOLLOW PAGE 192

INTRODUCTION

Civilized man has walked on the moon and is carrying out exploratory probes of outer space; yet there remain on earth two nearly unknown ecosystems —the depths of the oceans and the lowland tropical rainforest. Technological problems limit the exploration of oceans, but the tropical lowlands? Is the "foreboding jungle," to which the exaggerated writings of travelers and adventurers all-too-often refer, beyond the limits of modern technology?

In the Nineteenth Century a few naturalists ventured into the Amazon Basin in South America. The vast collections and provocative writings of Henry W. Bates, Alexander von Humboldt, Richard Spruce, and Alfred R. Wallace should have provided the impetus for continued and intensive exploration and study. Africa, with its relatively small Congo Basin, was the "dark continent" to be explored, colonized, and exploited, whereas South America, which so richly deserves the appelation given to Africa, languished. Although the short-lived "rubber boom" late in the last century left an opera house in Manáus, the Amazon Basin remained a biological *tierra incognita.*

Now the Amazon Basin is being exploited—before it has been adequately explored and studied. Human population pressure coupled with food and energy shortages seem to make it "practical" to settle the vast region, construct roads, clear the forests, cultivate the soil, and drill for oil. The lateritic soil is leached and eroded after two or three crops; the rivers are polluted; and we are losing forever a part of the world's biota. For the most part biologists are still ignorant of the fauna and flora of the Amazon Basin and have little accurate conception of the ecology of the rainforest. Ironically, the Biome Study Committee of the International Biological Program never succeeded in initiating a study of the tropical rainforest.

Today many biologists are concerned primarily with theoretical aspects of population biology, ecology, and evolution. Models of species diversity, niche breadth and overlap, resource partitioning, competition, predator-prey, and r and K selection abound in the literature. But how do these models apply to the tropics? Where and how can they be tested? Although inferences frequently are made in the literature, base line data are wanting in most cases.

The present report is an attempt to present base line data and preliminary interpretations. Hopefully, they will provide future investigators with the information and impetus for more intensive and varied ecological and populational studies, which in turn will furnish the bases for testing models. This report concerns the amphibians and reptiles of Santa Cecilia, a small area in the upper Amazon Basin. It deals with the amphibians and reptiles for two reasons. First, I am a herpetologist and am most knowledgeable about those groups. Second, amphibians and reptiles are ideal organisms for faunal study in the tropics. They are closely tied to the environment, usually are independent of given species of plants, and are sufficiently numerous and well enough known to be studied feasibly. The choice of the study area was completely fortuitous.

During the past ten years numerous publications dealing with the herpetofauna of the Santa Cecilia region have appeared. Many of these have been descriptions of new species: *Eleutherodactylus croceoinguinis* and *variabilis* (Lynch, 1968); *E. orphnolaimus* (Lynch, 1970); *E. martiae, paululus,* and *quaquaversus* (Lynch, 1974); *E. lanthanites* (Lynch, 1975); *Colostethus sauli* (Edwards, 1974); *Hyla brevifrons* (Duellman and Crump, 1974); *Hyla cruentomma* (Duellman, 1972a); *Centrolenella midas, munozorum,* and *resplendens* (Lynch and Duellman, 1973); *Chiasmo-*

cleis anatipes (Walker and Duellman, 1974); *Syncope antenori* (Walker, 1973); *Enyalioides cofanorum* and *Alopoglossus atriventris* (Duellman, 1973c); and *Helicops petersi* (Rossman, 1976). Other papers deal with the taxonomic status of various taxa: *Phrynohyas coriacea* (Duellman, 1968); *Hyla funerea* (Duellman, 1971b); *Hyla garbei* (Duellman, 1970a); *Hyla rhodopepla* (Duellman, 1972c); *Hyla punctata, rossalleni, leucophyllata* group and *Sphaenorhynchus carneus* (Duellman, 1974a); and Amazonian *Phyllomedusa* (Duellman, 1974b). Material from Santa Cecilia has been used in the following systematic reviews: *Hyla geographica* group (Duellman, 1973b); *Hyla parviceps* group (Duellman and Crump, 1974); *Hyla rostrata* group (Duellman, 1972b); *Osteocephalus* (Trueb and Duellman, 1971); *Hemiphractus* (Trueb, 1974); *Nyctimantis* (Duellman and Trueb, 1976); and Ecuadorian caecilians (Taylor and Peters, 1974). Fitch (1968) reported on body temperatures of several species of lizards. Crump (1974) provided a thorough analysis of reproductive strategies in the anurans, and Simmons (1975) analyzed the female reproductive cycle in *Ameiva ameiva*.

ACKNOWLEDGMENTS

Field studies were initiated at Santa Cecilia primarily because of the existence of a base camp, "Muñozlandia." Our work there was made possible by Ing. Ildefonso Muñoz B., who provided housing and a laboratory. He and his family made it possible for us to devote full time to biological studies while enjoying rustic, but comfortable, accommodations in the jungle. For their gracious hospitality, which included numerous *fiestas* and *despedidas*, I extend my sincere *muchissimas gracias* to the Muñoz family.

I am grateful to the personnel of Gulf Oil Ecuador and Texaco Petroleum Company, Ecuador, for providing air transportation between Quito and the Oriente and also for many other courtesies. Ecuadorian army personnel stationed at Santa Cecilia aided us in many ways; I am especially indebted to Colonel Ramirez. Our work in Quito was greatly facilitated by personnel at the Universidad Católica del Ecuador; I especially thank Father Gustavo Maldonado, Dra. Olga Herrera de MacBryde, and the late Francisco León.

Muñozlandia was "discovered" by Charles M. Fugler, formerly of Auburn University. I will be forever grateful to Fugler for his telephone call to me in October 1966 in which he suggested Santa Cecilia as a study site.

The data and specimens upon which this report is based were accumulated mostly by field parties from The University of Kansas. I thank each person for their contribution and list them in descending order of the amount of time spent at Santa Cecilia: Martha L. Crump, John E. Simmons, Linda Trueb, Stephen R. Edwards, James W. Waddick, Thomas H. Fritts, Charles F. Walker, John D. Lynch, Henry S. Fitch, Abraham Goldgewicht K., Werner C. A. Bokermann, Joseph T. Collins, Arthur C. Echternacht, and Robert W. Henderson. In addition to these persons, all of whom were primarily concerned with studies on the herpetofauna, I am indebted to Philip S. Humphrey, Stephen R. Humphrey, Frank B. Cross, Gerald R. Smith, and especially William G. Saul for their contributions made incidental to their studies on the birds and fishes. Charles M. Fugler, George Key, and Terry D. Schwaner collected amphibians and reptiles at Santa Cecilia; their specimens were deposited at Auburn University Museum and the Museum of Comparative Zoology at Harvard University. I am indebted to Schwaner for field notes and photographs and to Robert H. Mount and Ernest E. Williams for the loan of specimens. Charles F. Walker kindly made available material that he collected and deposited in the University of Michigan Museum of Zoology. Ronn Altig, Mississippi State University, collected at Santa Cecilia in 1973-1975; I am grateful to him for making material available to me.

Some of the limited information provided herein on the geology and vegetation was derived in part from information provided by Richard Govett of the Texaco Petroleum Company, John Dwyer of the Missouri Botanical Garden, and Bruce MacBryde, formerly of the Universidad Católica del Ecuador. I was fortunate in being able to spend time in the field with each of them.

The identification of the material collected at Santa Cecilia has been a long and arduous task that required visits to many museums; I am grateful to curators of these collections in the United States, Europe, and South America for their hospitality and provision of working space. Specimens of some groups have been studied by others, who have provided me with identifications and insights into the systematics of these groups. Thus, I am grateful to Edward H. Taylor (caecilians), Federico Medem (pleurodire turtles), Charles W. Myers (*Leimadophis* and *Rhadinaea*), Douglas A. Rossman (*Helicops*), W. Ronald Heyer (*Leptodactylus*), and Charles F. Walker (microhylids), and especially John D. Lynch for his efforts on the difficult genus *Eleutherodactylus*. I am extremely appreciative of the aid provided by the late James A. Peters, who on many occasions shared with me his extensive knowledge of the Ecuadorian herpetofauna.

The field studies were variously supported by the Herpetological Research Fund, F. William Saul Fund, and the Watkins Museum of Natural History Grants, all of The University of Kansas. Crump's field work in 1971-72 was supported by the National Science Foundation (GB-29557). Visits to European museums were made possible by a grant from the Penrose Fund of the American Philosophical Society (No. 5063), and part of the laboratory work was supported by a grant from the General Research Fund, The University of Kansas. A grant from the National Science Foundation (GB-35483) made possible the completion of the research.

During the preparation of this report I have been assisted by Jan Caldwell, Albert Fisher, Julian C. Lee, John E. Simmons, and especially Martha L. Crump. I sincerely thank them for their careful and extensive work. I am indebted to James R. Dixon and John D. Lynch for critically reviewing the taxonomic accounts and to Martha L. Crump for her provocative discussions and critical review of the manuscript. I am grateful to Juan R. León and Jaime E. Péfaur for translating the keys and summary into Spanish. Many of the photographs in this report were taken by Crump and Simmons; I thank them for permission to reproduce the photographs, and I am grateful to Simmons for his painstaking work in the darkroom.

Indeed I have been fortunate in having the opportunities to undertake this research and in having the cooperation of so many associates. But my most cherished fortune is my wife, Linda Trueb. She accompanied me on four trips to Santa Cecilia, assiduously worked in the field, and collaborated in several preliminary reports. She has provided many ideas for the organization, analysis, and interpretation of the data, and she has critically read the entire manuscript. But her major contributions to this report are her illustrations, the usefulness of which shall, I fear, long outlive my less colorful prose. Hers has been a labor of love, which I can never repay in kind.

SCOPE OF STUDY

The material presented herein is the result of 48 man months of field work at Santa Cecilia on the Río Aguarico, Provincia Napo, Ecuador, plus smaller collections of specimens and data from four nearby localities along the Río

TABLE 1.—Taxonomic Summary of the Herpetofauna of the Upper Río Aguarico, Ecuador. (The numbers given first are for the entire area; numbers in parentheses are for Santa Cecilia only)

ORDER: Family	Genera	Species	Specimens
GYMNOPHIONA			
Caeciliidae	4 (2)	5 (3)	65 (22)
CAUDATA			
Plethodontidae	1 (1)	2 (2)	122 (22)
ANURA			
Pipidae	1 (1)	1 (1)	8 (8)
Leptodactylidae	8 (8)	28 (25)	2109 (1602)
Bufonidae	2 (2)	4 (4)	473 (456)
Dendrobatidae	3 (3)	6 (5)	579 (526)
Hylidae	7 (7)	38 (37)	3060 (2859)
Centrolenidae	1 (1)	3 (3)	27 (20)
Ranidae	1 (1)	1 (1)	98 (97)
Microhylidae	4 (3)	6 (5)	111 (97)
TESTUDINES			
Cheliidae	4 (4)	4 (4)	18 (17)
Kinosternidae	1 (1)	1 (1)	9 (9)
Testudinidae	1 (1)	1 (1)	7 (3)
CROCODILIA			
Crocodylidae	2 (2)	2 (2)	16 (13)
SAURIA			
Gekkonidae	3 (3)	3 (3)	62 (47)
Iguanidae	5 (5)	11 (10)	849 (749)
Scincidae	1 (1)	1 (1)	44 (35)
Teiidae	12 (12)	14 (13)	823 (724)
AMPHISBAENIA			
Amphisbaenidae	1 (1)	1 (1)	6 (3)
SERPENTES			
Aniliidae	1 (1)	1 (1)	7 (3)
Boidae	4 (4)	5 (5)	21 (19)
Colubridae	26 (24)	38 (36)	459 (384)
Elapidae	2 (2)	5 (5)	18 (15)
Crotalidae	2 (2)	4 (4)	41 (35)
TOTALS	97 (92)	185 (173)	9035 (7765)

Aguarico. The area that was studied at Santa Cecilia consisted of about 3 square kilometers. During the course of the field work, efforts were made to collect series of each species from every month of the year and to obtain data on the microhabitat, activity, and life history of each species. As a result of the field work, 9035 specimens (+292 lots of tadpoles) representing 185 species were obtained; 7765 specimens (+288 lots of tadpoles) of 173 species are from Santa Cecilia (Table 1). These specimens and their accompanying data form the documentation for one of the richest herpetofaunas known from any one area in the world.

The bulk of this report is descriptive. Many of the species have never been described in detail, and most never have been illustrated. I present descriptions of the animals based on living colors and illustrations of most of the species. The tadpoles of 46 frogs are described. As an aid to the identification of species of amphibians and reptiles in the upper Amazon Basin, illustrated keys are offered in English and Spanish.

In attempting to analyze reproductive patterns and strategies I have summarized the data for all of the species and evaluated the data with respect to size of the animal, clutch size, mode of reproduction, and seasonality.

Perhaps the most interesting aspect of this report is the interpretation of the data with respect to the co-existence of so many species. Thus, in viewing resource utilization I have analyzed data on general habitat, structural habitat, diel and seasonal activity, and food. In concert with information on phylogenetic relationships and distributions of the component species, the ecological and reproductive data provide a basis from which an hypothesis on the evolution of this large tropical community is formulated.

Methods

All specimens were preserved in 10 percent formalin and subsequently stored in 70 percent ethanol, except tadpoles which were stored in formalin. Colors in life were noted in the field, and series of colored transparencies were taken. In the laboratory, animals were measured to the nearest millimeter. Gonads were examined only in females. Ovarian eggs were counted individually or in cases of frogs having several thousand eggs, a set volume was counted, and the total number was calculated on the basis of volume. Eggs were measured to the nearest 0.1 mm. Stomach contents were analyzed in 25 individuals (or as many as possible when 25 were not available) of each species. Prey items were identified to as small a taxonomic category as possible in vertebrates and to order in arthropods, save for gryllotalpids and blattids, which were distinguished from other orthopterans. The numbers of each kind of prey in a given stomach were noted, and the percentage volume of each kind was estimated.

Climatic data at Santa Cecilia were obtained from a rain gauge in a clearing and a maximum-minimum thermometer kept in a thatch-roofed building. Daily readings were taken at about 0800 hr each day. Because of the richness and complexity of the flora, no attempt was made at a floristic analysis; the vegetation was studied only in a structural context. Plant collections from Santa Cecilia exist in the Shaw Herbarium of the Missouri Botanical Garden in St. Louis and in the Herbarium, Universidad Católica del Ecuador in Quito.

Reliability and Limitations of Data

Ideally in a study of this sort, all of the data would be collected in precisely the same manner. Furthermore, equal amounts of time would be spent sampling different habitats throughout the year. However, such was not the case at Santa Cecilia, where our early field work (1966-1967) was devoted primarily to a faunal survey. Although data on the microhabitats and life histories of the species were obtained then, the data were not recorded in the coded framework utilized in the later field studies. Consequently, the amount of useable ecological data usually is less than the numbers of specimens indicate.

The greatest inconsistency in the data base is the unequal sampling throughout the year. Although one field party worked continuously at Santa Cecilia from June 1971 to July 1972, the other field parties were there for shorter periods of time and usually in June, July, and August. Thus, the number of man days of field work in July (309) is far greater than in many other months, especially January (39) and December (44). There is a corresponding disparity in the number of species and specimens from different months (Fig. 1). Consequently, conclusions concerning activity or reproduction of a given species are biased by the few data from some months (January and December especially). Accordingly, if some females of a given species are gravid in every month, except January and December, months from which only one or two nongravid females are available, I have been inclined to state that the species breeds throughout the year. On the other hand, the absence of gravid females in July is considered to be valid.

Although field studies were conducted throughout the year, the collecting of tadpoles was sporadic. Consequently,

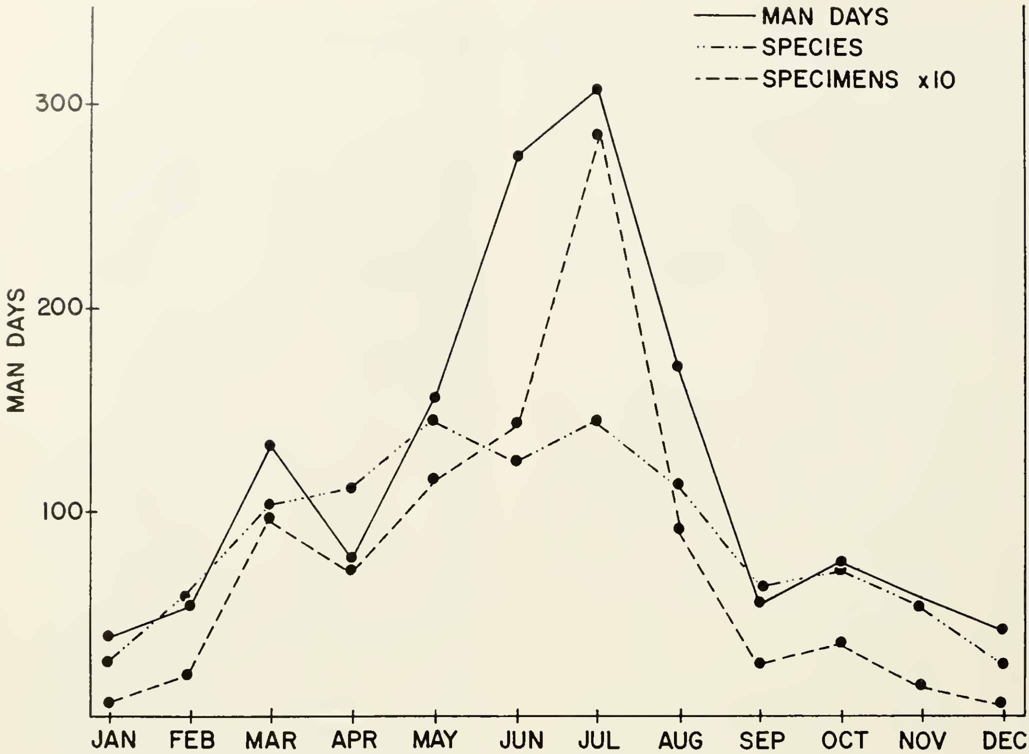

FIG. 1.—Comparative monthly rates of collecting effort and results at Santa Cecilia.

data on occurrence of tadpoles was used only in a positive way—*i.e.*, absence of data on tadpoles in a given habitat or at a time of the year was not considered to be reliable.

DESCRIPTION OF THE AREA

The Amazon Basin, with an area of about 6,000,000 square kilometers, straddles the equator and extends from the base of the Andes about 3000 kilometers eastward to the Atlantic Ocean. With the exception of some low hills and plateaus, the elevation diminishes gradually from about 500 meters at the base of the Andes to sea level at the mouth of the Amazon. Although Ecuador is a small country with a coastline on the Pacific Ocean and with the Andes bissecting the country from north to south, approximately one-third of the country lies in Amazon Basin (Fig. 2), a region referred to locally as the Oriente. The major river in the Oriente is the Río Napo, which flows southeastward to join the Río Marañón near Iquitos, Perú, and form the Rio Solimões. The latter flows eastward to Manáus, Brasil, where it is joined by the Rio Negro to form the great Rio Amazonas.

One of the major tributaries of the Río Napo is the Río Aquarico; the latter is formed by the confluence of the Río Cofanes and the Río Chingual, both of which drain the eastern face of the Andes in northern Ecuador. The confluence is at an elevation of 600 meters; from this point the Río Aguarico flows rapidly in a boulder-strewn bed to a point below Santa Cecilia (340 m). Throughout the remaining two-thirds of the length of the river, it is broad, primarily silt-bottomed, and drops to an elevation of about 200 meters at its confluence with the Río Napo.

Geologically the region of the upper

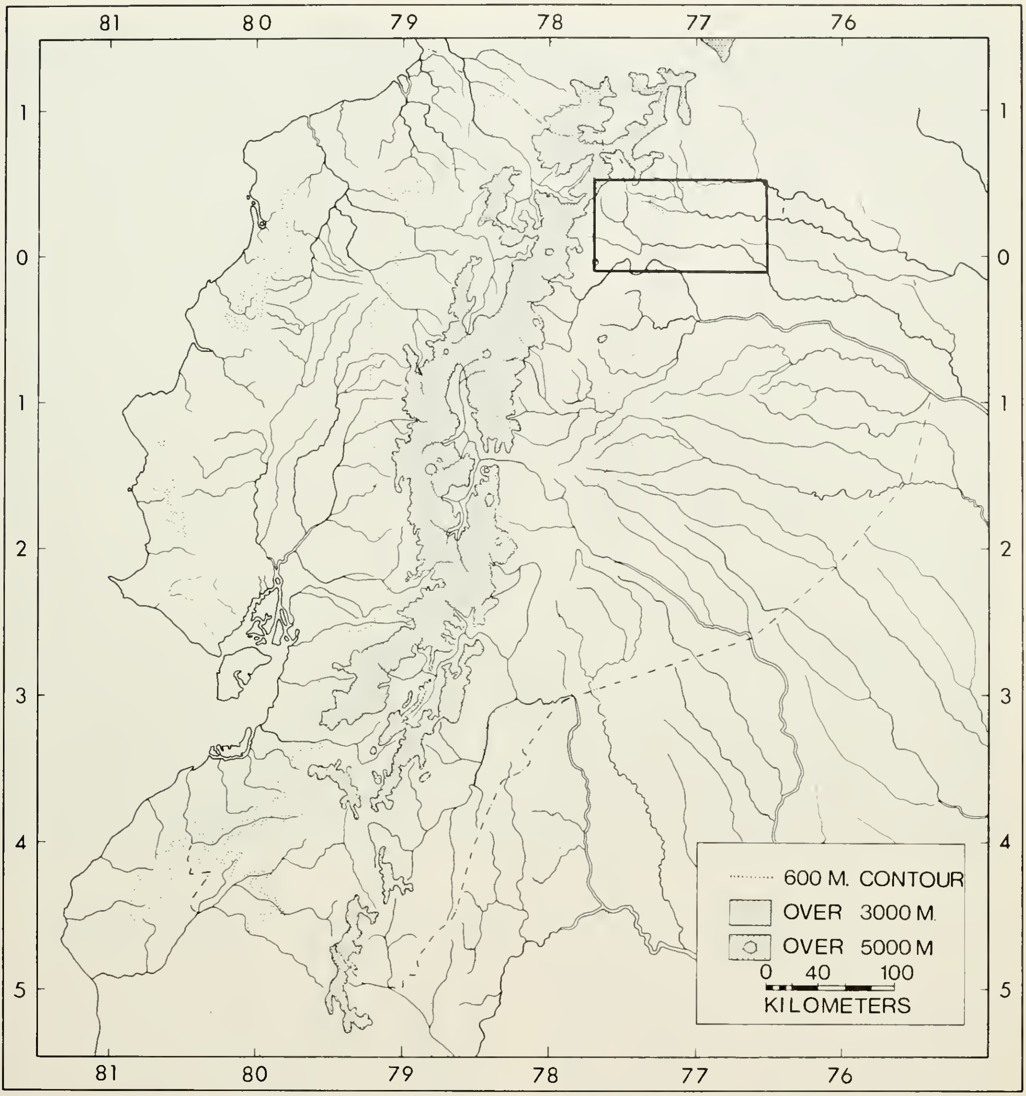

FIG. 2.—Map of Ecuador showing location of the upper Río Aguarico area.

Río Aguarico consists of deep Tertiary alluvial deposits (2500-3000 m) above Cretaceous marine sandstones (Tschopp, 1953; Harrington, 1962). Following the terminology of Beek and Bramao (1969), two principal soil types occur in the region. Closest to the Andes and continuing eastward in the well-drained areas are reddish brown laterites, whereas red-yellow podzols occur in poorly drained areas removed from the Andes. Pale yellow latosols and low humic gley soils occur in extreme eastern Ecuador, but apparently these either are absent or inconspicuous in the region studied. The beaches along the Río Aguarico are quartz sand or river pebbles. The average size of the latter varies from about 30 cm near the base of the Andes to about 10 cm at Santa Cecilia.

Whereas the primary study area consisted of about 3 square kilometers at Santa Cecilia, four other sites along the Río Aguarico were included as secondary

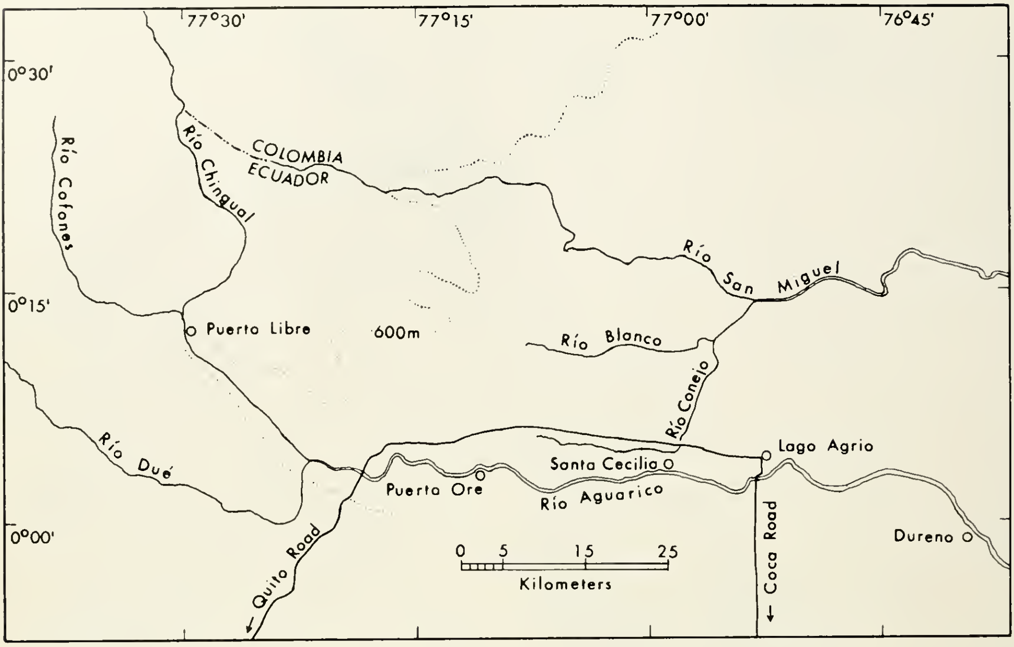

FIG. 3.—Map of the upper Río Aguarico showing location of study sites.

study areas; together these encompassed an airline distance of about 85 kilometers and an elevational range of 320-570 meters (Fig. 3). The five sites are described below:

Dureno.—00°02'S, 76°30'W; 320 m. This small Cofan Indian village is on the south bank of the Río Aquarico. A few hectares around the village were cultivated; elsewhere there was primary forest (1967).

Lago Agrio.—00°03'N, 76°53'W; 340 m. This is now the major petroleum center in the Oriente of Ecuador with a large airfield, refinery, and town of about 2500 people. When field work was done there (1969), the area was virgin primary forest. This site should not be confused with a small lake by the same name about 3 kilometers to the northwest.

Puerto Libre.—00°12'N, 77°29'W; 570 m. This is an intermittent placer mining camp with a grass airstrip situated in a narrow valley at the base of the Andean foothills. In 1968 there was secondary forest in the immediate vicinity of the camp; elsewhere the area was covered by primary forest.

Puerto Ore.—00°03'N, 77°11'W; 420 m. This was a temporary placer mining camp on the south bank of the Río Aguarico. The area mostly supported primary forest (1968).

Santa Cecilia.—00°03'N; 76°59'W; 340 m. Prior to 1965 this was a small Quecchua Indian village scattered along the north bank of the Río Aguarico. In 1965, Texaco-Gulf established a petroleum exploration camp and built an airstrip. When field studies were initiated in November 1966 most of the area was covered by primary forest (Fig. 4). The exceptions were the clearings for the airfield, exploration camp, and the two-hectare compound "Muñozlandia", which served as our base camp. Adjacent to the village of Santa Cecilia were some fields of *plátanos* and *yuca*. All human habitation and disturbance were between the Río Aguarico and the much smaller Río Conejo lying 1-2 kilometers to the north. The Río Conejo flows northward into the Río San Miguel, a tributary of the Río Putumayo, which is a large river flowing eastward into the Rio Solimões. Beginning in 1966 each succeeding year

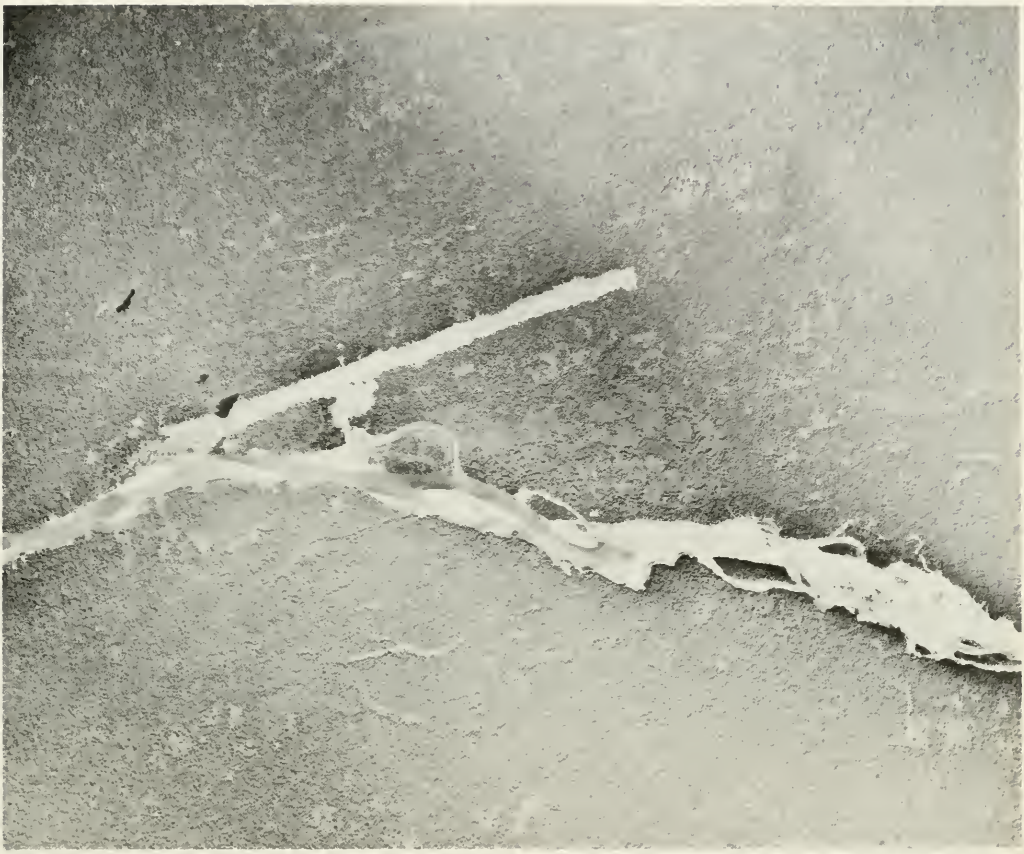

FIG. 4.—Aerial photograph of the Río Aguarico encompassing the village of Santa Cecilia on the north bank of the river at the left edge of the picture and the airstrip (diagonal clearing in middle of picture). The darker irregular tones are forest; the pale areas are swamps dominated by *Heliconia*. Photographed 2 February 1966 (courtesy of U.S. Air Force).

brought more people into Santa Cecilia and more destruction of the forest, so that by 1971 many farms of 50 or more hectares had been hacked out of the forest. In October 1971 the road between Quito and Lago Agrio was completed; the oil companies moved to Lago Agrio, and the Ecuadorian army took over the oil camp (Fig. 5). With the completion of the road, most of the families that had been living on the river bank moved to the road; in so doing, they abandoned their homes and cultivated areas. Thus, Santa Cecilia, as a village no longer exists. Many of its former inhabitants now own 50-hectare homesteads along the road.

Unless specified otherwise, the information in the following sections pertains only to the area of Santa Cecilia.

Physiography and Hydrography

The terrain is generally flat with numerous small streams and depressions; the total relief is about 20 meters. The airstrip occupies a narrow ridge between the Río Aguarico and Río Conejo. From Muñozlandia eastward the ridge gradually diminishes to the Río Aguarico, but upstream there is a bluff along the river. The higher ground encompasses most of the area between the Río Conejo and the Río Aguarico west of the airstrip.

The Río Aguarico is a "white water" river with a width of about 100 meters at Santa Cecilia. According to Saul

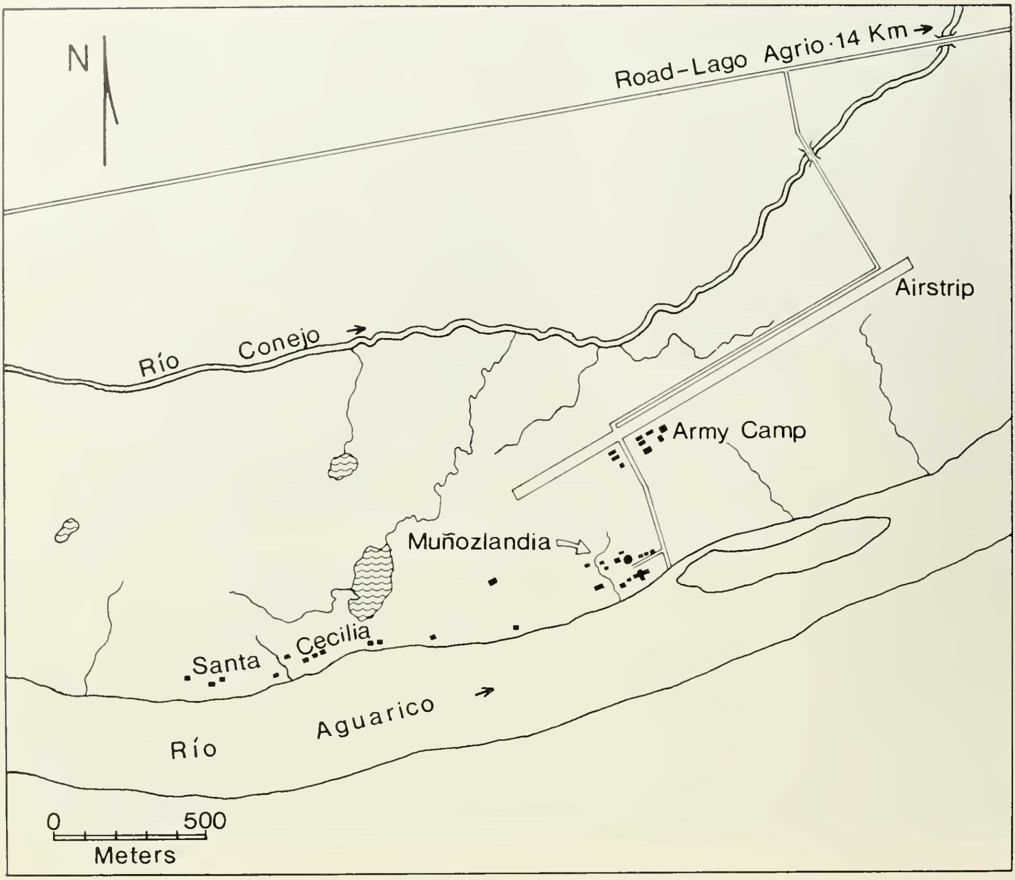

FIG. 5.—Map of the study area at Santa Cecilia. All work was done between the Río Aguarico and the Río Conejo and from the small lake at the extreme left to the eastern end of the airstrip.

(1975), the velocity frequently exceeds 2.0 meters per second, and the surface temperature varies between 18° and 20° C. Water level fluctuations of about 5 meters were common and mostly associated with heavy rains on the Andean slopes. At times of high water, the size of the island at Santa Cecilia was markedly reduced, and local residents claimed to have seen the entire island covered with water. In contrast, at times of low water a broad, boulder and silt bar connects the western end of the island with the north bank of the river (Fig. 6), resulting in an extensive backwater lagoon on the north side of the island.

The Río Conejo is a shallow (up to 2 meters), meandering stream about 6 meters in width. In undisturbed areas the river is concealed by the forest. The velocity is 0.3-0.6 meters per second, and the surface temperatures are 22-23° C. (Saul, 1975). Other streams in the area are small (< 3 meters wide) and shallow. They vary in gradient from some spring-fed rivulets that descend over rock and gravel from the ridge to the Río Aguarico to silt-bottomed streams draining lakes and swamps.

Two permanent lakes are present in the area. The southern lake is the largest (± 150 × 300 m), whereas the northern is about 100 m in diameter. Both lakes are deep; actual depths are unknown but exceed 10 m. Originally these eutrophic lakes were bordered by

FIG. 6.—The Río Aguarico, looking downstream from Muñozlandia. In the foreground is the bar extending to the island at a time of low water.

primary forest (Fig. 7). Surface temperatures of the southern lake fluctuate daily from 23.8° to 27.8° C (Saul, 1975). A smaller, shallow lake (± 25 × 75 m) exists in the western part of the study area. Infrequently it is reduced to a small, muddy pool.

There are numerous swamps in depressions, and after heavy rains these and other low-lying areas offer extensive aquatic habitats that are drained by the numerous small streams.

CLIMATE

The climate at Santa Cecilia is typically *Af* in the Köppen classification, the climate type characteristic of the upper Amazon Basin (Eidt, 1969). Here we have essentially an aseasonal climate. This is not to say that fluctuations do not occur, but there are no distinct seasons. The only complete year of climatic data is for the period 29 June 1971 through 14 July 1972 (Fig. 8; Table 2). The following discussion also includes data from June-July, 1967, June-August, 1968, April-May, 1969, and April-May, 1973.

Winds are uncommon at Santa Cecilia; as often as not, a heavy rain may be preceded by a gentle breeze. Day length is nearly constant, and effective daylight is controlled more by cloud cover than by the seasonal position of the sun.

The daily temperature fluctuation is usually about 10° C. The greatest daily fluctuation recorded was 22-37° C on 9 August 1968; this also was the highest temperature recorded. The least fluctuation was 21.5-23.0 C on 22 April and 18 June 1972. The lowest temperature (17.0° C) was on the night of 17 June 1968. The lowest daily maximum temperatures and the lowest daily fluctuations are during periods of several days of continuous heavy cloud cover. Conversely, the highest daily maximum tem-

FIG. 7.—The west shore of the lower lake at Santa Cecilia.

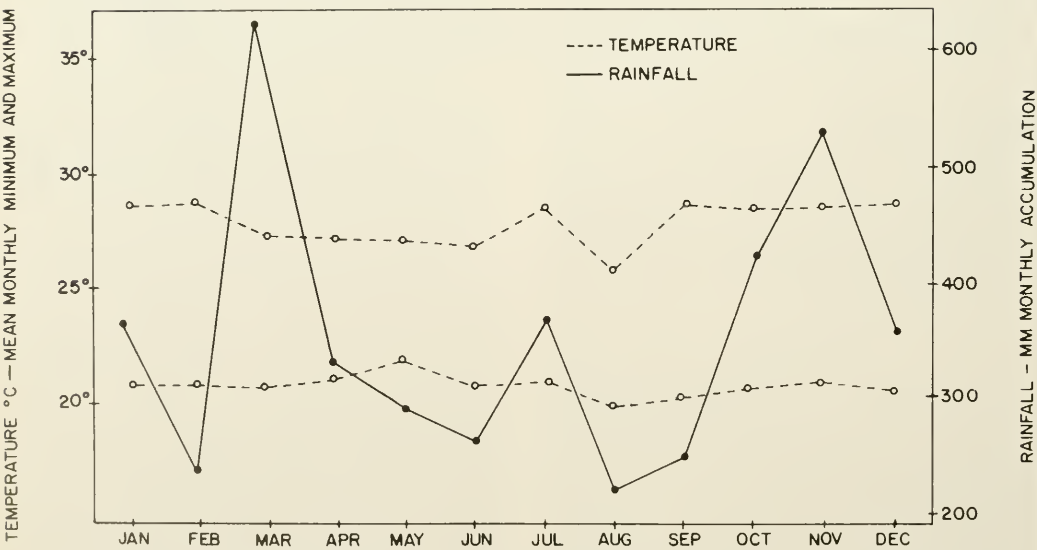

FIG. 8.—Monthly mean minimum and maximum ambient air temperatures and monthly rainfall accumulation at Santa Cecilia for the period July 1971-June 1972.

TABLE 2.—Summary of Climatic Data from Santa Cecilia.
(July 1971-June 1972)

Month	Rainfall (mm) Amount	Mean/Day	Days	Cloud Cover (Days) Heavy	Clear	Temperature (° C) Maximum	Minimum
Jan	372.5	12.0	22	8	7	24.5-30.0	19.0-23.0
Feb	243.0	8.4	17	10	4	24.0-31.5	18.5-23.0
Mar	619.0	20.0	25	12	9	23.0-35.0	19.0-23.0
Apr	340.0	11.3	21	21	3	23.0-32.0	18.0-23.0
May	306.5	10.0	25	14	3	23.0-31.0	20.0-23.0
Jun	250.5	8.4	21	9	7	23.0-31.0	18.5-23.0
Jul	367.0	11.8	23	7	3	24.0-32.5	20.0-23.0
Aug	220.5	7.1	20	24	4	22.0-31.0	18.0-22.0
Sep	251.5	8.4	21	19	4	23.0-33.0	18.5-22.0
Oct	422.0	13.6	25	13	4	23.5-32.0	18.0-22.0
Nov	530.5	17.7	21	16	6	23.0-32.0	20.0-23.0
Dec	366.5	11.8	17	3	15	24.0-32.5	19.0-22.0
TOTAL	4289.5	......	215	156	69	22.0-35.0	18.0-23.0

peratures and the greatest daily fluctuations are during periods of clear weather.

Rainfall is abundant, but erratic; 4390 mm of rain were recorded in one year (Table 2). Local residents claim that normally August-September and December-February are drier than other times and that April-May and October-November have the heaviest rains. These observations are at least partially substantiated by data from 1971-1972, although in 1972, March with 619 mm of rain was the wettest month. In the period 3-23 March 1972 there were 393 mm of rain; in the same period in 1967 there were only 150 mm. Although in April-May 1972 there were only 646.5 mm of rain, the contention of the local residents was borne out in 1973, when 1335.5 mm fell in 30 days (Table 3). December 1971 was a relatively dry month with only 234 mm of rain in the first 29 days, but 114 mm fell on December 30. The only other records of rainfall in excess of 100 mm in a 24 hr period were in 1973: 26 April (390 mm), 1 May (105 mm), and 8 May (165 mm). Among the rainfall records for 20 months at Santa Cecilia, there are six instances of rainfall on more than ten consecutive days: 15-27 June 1967, 130 mm (1-34/day); 10-20 July 1968, 171 mm (2-46/day); 6-19 October 1971, 209 mm (1-54/day); 29 December 1971-9 January 1972, 281 mm (1-114/day); 8-21 May 1972, 166 mm (1-54/day); 29 April-9 May 1973, 614 mm (2-165/day).

The number of consecutive days without rain varied from one in May to five in December, although there were more days that were predominately clear. The greatest number of consecutive clear days was nine in December. The rainfall pattern usually consists of three or four rainy days with a maximum of 50-70 mm for the period and a maximum of 30-50 mm on any given day, followed by one or two days without rain. The general pattern does fluctuate, however, and sometimes there are 8-10 consecutive days of moderate to heavy cloud cover with only 1-5 mm of rain each day. Conversely, it is possible to have several consecutive days of heavy rainfall, such as 29 April-5 May 1973, in which the daily rainfall was 70, 19, 105, 29, 90, 42,

TABLE 3.—Comparative Rainfall Data (mm) for Three Years.

	10 June-9 July		
Year	1967	1968	1972
Total	322.0	304.0	330.5
No. Days	23	22	21
Daily Mean	10.7	10.1	11.0
Daily Range	0–71.0	0–50.0	0–22.5
	19 April-18 May		
Year	1969	1972	1973
Total	378.0	316.0	1335.5
No. Days	20	24	22
Daily Mean	12.6	10.5	46.6
Daily Range	0–45.0	0–53.5	0–390.0

FIG. 9.—Aerial view of Santa Cecilia looking northeast. The Río Aguarico is visible in the lower right corner.

and 17 mm. This was followed by 2, 71, 165, and 4 mm, 3 days with no rain, and then 86, 38, and 46 mm. Generally, rain falls more frequently by day than at night. Rain was recorded on 215 days in the period July 1971-June 1972; of these, rain fell during the day and night on 47 days and only at night on 40 occasions. Sometimes rainfall is extremely localized during brief but heavy showers, whereas at times of extensive heavy cloud cover the entire region receives rain.

VEGETATION

Although plant collections have been made for the Shaw Herbarium of the Missouri Botanical Garden in St. Louis and the herbarium at the Universidad Católica in Quito, no published summary of the flora is available. Because the physiognomy determines the numbers and kinds of habitats available for animals, the following commentary is concerned more with the structure of the vegetation than with the floristics.

Santa Cecilia is near the western limits of the largest expanse of tropical rainforest in the world. This biotope called the *Hylea* by most South American biologists is referred to locally as the *selva.* The region of Santa Cecilia is at a sufficiently high elevation to preclude the seasonal flooding of great expanses of forest. Thus, the *bajiales* of the lower elevations of the Amazon Basin, characteristic as far inland as Iquitos, Perú, are absent.

Prior to 1965 we can assume that, with the exception of a few clearings along the river and scattered swamps, the entire region was covered with primary rainforest (Fig. 9-10). This forest is best developed on level, well-drained ground. In such places the largest trees form a canopy 30-35 meters above the ground. Some stilt palms protrude through the canopy. The largest trees in the primary

FIG. 10.—Aerial view of Muñozlandia. The Río Aguarico is to the left. The large square building in the upper center is the laboratory.

forest are scattered 30-50 meters apart. Most such trees have extensive buttresses, that may extend 3 meters up the trunks, which may be up to 2 meters in diameter (Figs. 11-12). In some areas definite stratification can be found. A secondary stratum, when present, is 15-20 meters above the ground. This usually consists of broad-leafed trees, with or without buttresses, and stilt palms. A third layer at 8-12 meters consists of smaller, broad-leafed trees and spiny palms. The ground cover consists of a great variety of broad-leafed herbs 10-25 cm high and small ferns. In the primary forest there is a deep (5-10 cm) and continuous mulch layer. At midday usually no more than 10 percent of the ground cover receives sunlight. Lianas are numerous, and heavy growths of epiphytes are present on the horizontal limbs of the large trees, although bromeliads are uncommon. The large, buttressed trees forming the canopy have shallow, extensive root systems. Growth seems to be limited by the ability of the shallow soil to hold the towering trees. These forest giants frequently fall over, with the uprooting of the extensive root system creating broad shallow craters and the interwoven system of lianas tearing a large swath in the forest. Thus,

FIG. 11.—Buttressed base of large tree in primary forest.

FIG. 12.—A trail through primary forest. Note the abundance of lianas.

Fig. 13.—Secondary forest. The large-leafed trees are *Cecropia.*

FIG. 14.—A forest-edge situation showing dense shrubby growth; in the foreground is a marsh.

there are numerous natural clearings in the primary forest.

Clearings, either natural or man-made, soon are overgrown by bushes, saplings, and the successional *Cecropia*. These trees attain heights of 10-12 meters. The secondary forest is characterized by dense, bushy undergrowth, few lianas, epiphytes, and herbs, and little mulch (Fig. 13). At the edge of either primary or secondary forest, especially along the borders of man-made clearings, there is a dense growth of various successional plants, especially leafy vines, which form an impenetrable wall of vegetation (Fig. 14).

Stands of bamboo with individual stalks reaching heights of 15-18 meters are scattered through the forest, although bamboo is uncommon in climax primary forest (Fig. 15).

FIG. 15.—Bamboo grove in secondary forest.

Within both primary and secondary forest there are depressions that contain water at least intermittently. These swamps vary from small, shallow depres-

FIG. 16.—A forest swamp that contained water throughout most of the year.

sions that are flooded only after heavy rains to large semi-permanent swamps (Fig. 16). The swamps in primary forest characteristically have numerous spiny palms, whereas the swamps in secondary forest usually support dense growths of *Heliconia,* the immense leaves of which attain lengths of 2 meters, exclusive of stems (Fig. 17).

Man-made clearings are either cultivated or maintained as clearings by man or grazing animals. Some *maiz* and pineapple are grown, but *plátanos* and *yuca* are the most common crops. As a result of topographic irregularities, there are low-lying areas in clearings that contain water. The marshes in these open depressions contain sawgrass, small *Heliconia,* and various aroids (Fig. 18).

HABITATS

Throughout the accounts of the species and in the ecological analysis, the data are organized by major types of habitat. These are defined as follows:

Primary Forest.—Mature forest characterized by nearly continuous canopy, stratification of vegetation, and deep mulch layer.

Secondary Forest.—Successional stages and partially lumbered primary forest. The cutting of the large trees results in a physiognomy resembling that of intermediate successional stages.

Forest Edge.—The ecotone, usually resulting from human disturbance, between forest and clearings.

Bamboo.—Any of the stands of bamboo in forest or cleared areas.

Clearing.—Uncultivated clearings, usually man-made and characteristically supporting a variety of grasses.

Cultivated Fields.—Any cleared areas bearing crops.

Swamp.—Forest depressions containing water either ephemerally or permanently.

Fig. 17.—Dense growth of *Heliconia* in a shallow swamp.

Fig. 18.—A forest-edge marsh with a thick growth of sawgrass.

Marsh.—Water-filled depressions in clearings.

Lake.—This category includes only the two permanent lakes in the area.

River.—Only the two major waterways (Río Aguarico and Río Conejo) are included in this category.

Stream.—All flowing water not included in the former category.

IDENTIFICATION OF THE SPECIES

One of the most difficult problems that faces biologists working with the large Amazonian biota is the identification of the species. The following keys are offered as an aid to the identification of the species of amphibians and reptiles from the upper Río Aguarico. They should be useful for the herpetofauna of the entire upper Amazon Basin in Ecuador, southern Colombia, and northern Perú. Identifications made by use of the keys should be checked against the descriptions given in the accounts of the species.

The keys have been designed for use in the field with living or freshly preserved specimens. Unless stated otherwise, colors pertain to living animals. All characters used in the keys are visible with no more magnification than that provided by a 10× hand lens. The keys are satisfactory for specimens of all ages, except that some juvenile frogs will present difficulties.

All character states, except the most obvious ones, are illustrated. Internal structures, such as dentition and hemipenes, have been avoided. The most confusing scutellation character in snakes is the loreal, a scale on the side of the head between the nasal and the preocular (Fig. 41a). Some snakes lack either the loreal scale or the preocular scale. If the scale that is present is higher than long, it is the preocular (Fig. 41c), whereas, if it is longer than wide, it is the loreal (Fig. 43b).

Uno de los problemas más difíciles que han enfrentado los biólogos a trabajar con la abundante biota amazónica ha sido la identificación de las especies. Las siguiente claves se entregan como una ayuda para la identificación de las especies de anfibios y reptiles de la region del alto Río Aguarico. Ellas deberían ser igualmente útiles para la herpetofauna de toda la Hoya Amazónica tanto en Ecuador, el sur de Colombia, como en norte de Perú. Las identificaciones hechas a través de estas claves deberían ser confrontadas con las descripciones dadas en los registros de especies.

Estas claves han sido diseñadas para su uso en el campo, trabajando con especímenes vivos o recientemente preservados. Si no menciona otra cosa, las colores corresponden a animales vivos. Todos los caracteres usados en las claves son visibles con no más aumento que el dado por una lupa manual de 1OX. Las claves con satisfactorias para especímenes de toda edad, excepto para algunos sapos juveniles que presentarán un poco más de dificultad.

Todos los caracteres señalados, excepto los más obvios, son ilustrados. Las estructuras internas, tales como dentición y hemipenes, han sido evitados. De los caracteres de escutelación el que más confunde en las culebras es la escama loreal, ubicada lateralmente en la cabeza entre las escamas nasal y la preocular (Fig. 41a). En algunas culebras la loreal o la preocular están ausentes; en tal caso, si la escama presente es más alto que larga, es la preocular (Fig. 41c); si fuese más larga que ancha, correponde a la loreal (Fig. 43b).

Key to the Turtles

1. Neck folds laterally to lie along margin of shell ... 2

   Neck withdraws straight back into shell ... 5

2. Head broad, flat, with fleshy proboscis and many long barbels; carapace broad, depressed, with ridges of keeled scutes ... *Chelus fimbriatus* (p. 192)

   Not as described ... 3

3. Two rounded, longitudinal ridges on carapace; lateral edges of carapace upturned ... *Platemys platycephala* (p. 193)

   Not as described ... 4

4. Margin of posterior plastral indentation concave (Fig. 27a); plastron dark; throat dusky ... *Mesoclemmys gibba* (p. 192)

   Margin of posterior plastral indentation convex (Fig. 27b); plastron pale with or without dark spots; throat cream with black spots ... *Phrynops geoffroanus tuberosus* ... (p. 193)

Clave de la Tortugas

1. Cuello plegado lateralmente fuerca de la concha ... 2

   Cuello se retrae directamente dentro la concha ... 5

2. Cabeza ancha, chata, con proboscis carnosa y muchas barbillas; carapacho ancho, deprimido, con las salientes de los escutelos quillados ... *Chelus fimbriatus* (p. 192)

   Diferente a lo descrito ... 3

3. Dos crestas longitudinales redondeadas en el carapacho; márgenes laterales del carapacho dispuestos hacia arriba ... *Platemys platycephala* (p. 193)

   Diferente a lo descrito ... 4

4. Márgen de la identación plastral posterior cóncava (Fig. 27a); plastrón oscuro; región gular terrosa ... *Mesoclemmys gibba* (p. 192)

   Márgen de la identación plastral posterior convexa (Fig. 27b); plastrón pálido con o sin manchas ascuras; región gular crema con manchas negras ... *Phrynops geoffroanus tuberosus* ... (p. 193)

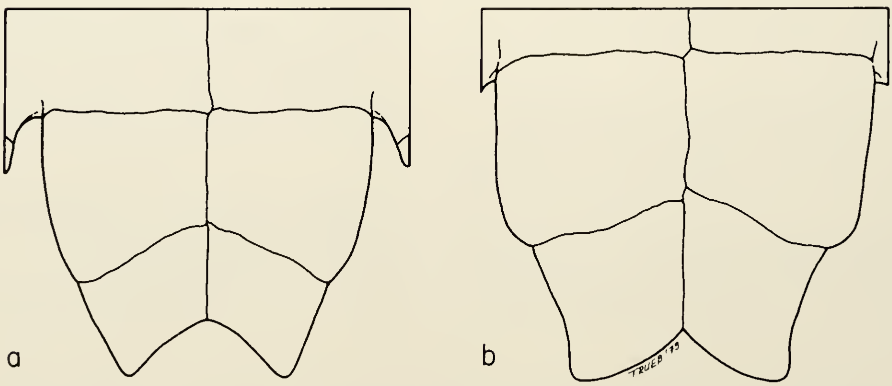

Fig. 27.—Posterior margins of plastra: A. *Mesoclemmys gibba*, B. *Phrynops geoffroanus*.

Syncope antenori Walker

Syncope antenori Walker, 1973, Occas. Pap. Mus. Nat. Hist. Univ. Kansas, 20:3 [Type locality.—Puerto Libre, Provincia Napo, Ecuador].

Material.—Puerto Libre, 11.

Identification.—This minute, dull microhylid frog differs from all other frogs in the area by having only four toes and, additionally, from all other microhylid frogs by having a visible tympanum.

This small frog has a robust body and broadly truncate snout in dorsal view. The distinct tympanum is about half of the diameter of the eye. The fingers bear lateral fringes; the four toes (the normal first toe absent) have terminal discs and lack webbing. The dorsum is dull brown; the venter is grayish brown with small bluish white flecks. Males lack nuptial excrescences. ♂ 12 mm; ♀ 14 mm.

Occurrence.—Eight individuals were in primary forest and three in secondary forest in July. All were found at night – four on leaves of low herbs and seven on the ground.

Life History.—Five females contained 5-6 ($\bar{X}$=5.4) ovarian eggs 1.2 mm in diameter. The presence of few relatively large ovarian eggs suggests that in this species eggs may be terrestrial and undergo direct development.

Mating Call.—No call was associated with this species. The absence of vocal slits in adult males perhaps is indicative that this small frog is mute.

Food.—Examination of seven stomachs revealed the presence of ants and mites in six; one of these also contained a small beetle. The seventh individual contained a beetle, a diplopod, and a pseudoscorpion.

TURTLES

Chelidae

Chelus fimbriatus (Schneider)

Testudo fimbriata Schneider, 1783, Allgem. Naturgesch. Schildkr.:349 [Type locality.—Surinam].

Chelys fimbriata—Boulenger, Cat. Chelon. Rhynchoceph. Crocod. Brit. Mus.:209.

Chelus fimbriatus—Mertens, Müller, and Rust, 1934, Bl. Aqua.-Terr. Kunde, 45:65.

Material.—Santa Cecilia, 3.

Identification.—This flattened turtle, commonly called *matamata,* with a broad head and fleshy proboscis is unlike any other Amazonian turtle. The snout and parietal region are orange-tan; the rest of the head and neck are dull dark brown. The limbs are dark brown with a tan stripe along the anterior edge of the forelimb. The carapace is dark brown with a yellowish tan middorsal stripe; the tips of the keels on costal and and marginal scutes are tan. The plastron is dull tan. ♂ 330 mm; ♀ 345 mm.

Occurrence.—All of the specimens were obtained from the Río Aguarico by Indians.

Life History.—No data are available.

Mesoclemmys gibba (Schweigger)

Emys gibba Schweigger, 1812, Königsberg. Arch. Naturgesch. Math., 1:299 [Type locality.—unknown].

Mesoclemmys gibba—Gray, 1873, Ann. Mag. Nat. Hist., (4) 11:306.

Material.—Santa Cecilia, 5.

Identification.—This side-necked turtle has a smooth, broad carapace that is flared laterally. It differs from *Phrynops* by having a dark plastron (light in *Phrynops*) and from *Platemys* by having a smooth carapace (two rounded longitudinal ridges in *Platemys*). Furthermore, *Mesoclemmys* has a shallow rounded indentation in the posterior margin of the carapace, whereas *Phrynops* has a deep angular indentation. The carapace and plastron are dark brown to black, and the head and neck are brown. ♀ 214 mm.

Occurrence.—Two were brought in by natives, and two shells were found by a forest pond. Another was in a marsh in a clearing.

Life History.—No data are available.

Remarks.—The two recently killed females were found by a pond in primary forest in April; only shells remained. Conceivably these individuals were seeking oviposition sites when they were attacked by predators. The proximity of the turtles to the large permanent pond suggests that this species may inhabit such ponds and lakes.

Phrynops geoffroanus tuberosus (Peters)

Platemys tuberosa Peters, 1870, Sber. Akad. Wiss. Berlin, 1870:311 [Type locality.—Cotinga River, Mt. Roraima, Guyana].
Phrynops geoffroana tuberosa—Müller, 1939, Physis, 16:95.

Material.—Puerto Ore, 1; Santa Cecilia, 1.

Identification.—*Phrynops geoffroanus* has a broad, smooth carapace that is flared peripherally. The carapace has a deep angular indentation in the posterior margin. The carapace is black. The plastron and ventral flange of the carapace are creamy yellow to orange with black spots. The limbs are dull gray with pale red to creamy white spots. The head and neck are dull olive green with fine black reticulations and a black line from the snout through the orbit and onto the neck. The throat is pale tan with irregular black markings. A pair of long creamy white chin barbels are present. The only other side-necked turtle in the area with a smooth carapace is *Mesoclemmys gibba* which has a black plastron with a shallow rounded indentation in the posterior margin. ♀ 316 mm.

Occurrence.—Both specimens were obtained from the Río Aguarico by natives.

Life History.—No data are available from Santa Cecilia. Medem (1969:334) reported nests containing 10, 11, and 15 eggs found in March and November in Caquetá, Colombia.

Platemys platycephala (Schneider)

Testudo platycephala Schneider, 1792, Schr. Ges. Naturf. Freunde Berlin, 10:261 [Type locality.—"East Indies"].
Platemys platycephala—Boulenger, 1889, Cat. Chelon. Rhynchoceph. Crocod. Brit. Mus.: 227.

Material.—Santa Cecilia, 8.

Identification.—This brightly colored turtle is readily distinguished from other side-necked turtles in the area by its elongate carapace having two rounded longitudinal ridges, bordering a median depression. The shells of *Mesoclemmys* and *Phrynops* lack ridges, and *Chelus* has three keeled ridges. The carapace, plastron, and skin are dark brownish black with an orange-tan periphery to the shell and broad orange stripes on the limbs and dorsum of the head. ♂ 161 mm; ♀ 156 mm.

Occurrence.—A juvenile having a carapace length of 55 mm was in a patch of sunlight in a shallow rivulet in primary forest, and one adult was crawling along a trail by day. One adult was in shallow water in the Río Aguarico by day, and two adults were lying on the bottom of shallow swamps at night.

Life History.—No data are available.

Kinosternidae

Kinosternon scorpioides (Linnaeus)

Testudo scorpioides Linnaeus, 1766, Systema Naturae, Ed. 12, 1:352 [Type locality.—Surinam].
Kinosternon scorpioides—Gray, 1831, Synops. Rept., 1:34.
Cinosternon scorpioides scorpioides—Siebenrock, 1907. Sber. Akad. Wiss. Wien, 116: 576.

Material.—Santa Cecilia, 9.

Identification.—This small turtle with a high carapace with three low, longitudinal keels withdraws the neck into the shell. Other species with longitudinal ridges or keels on the carapace (*Chelus* and *Platemys*) have low, flattened shells, and fold the neck laterally under the margin of the shell. The other turtle with a high carapace is *Geochelone*, which has short limbs with unwebbed toes; the toes of *Kinosternon* are webbed. The carapace is dull grayish brown; the plastron is dull yellowish brown. The top of the head is yellowish orange with black flecks; the rest of the head, neck, and limbs are dull gray. ♂ 161 mm; ♀ 155 mm.